Global Environmental Change 53 (2018) 24–38

Contents lists available at ScienceDirect

Global Environmental Change

journal homepage: www.elsevier.com/locate/gloenvcha

Disentangling effects of climate and land-use change on West African drylands' forage supply

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ARTICLE INFO

Keywords:
Global change
Savanna ecosystem
Metabolisable energy
Fodder biomass
Social-ecological system (SES)
Structural equation modelling (SEM)

ABSTRACT

Livestock rearing is the most important agricultural activity in global drylands, making forage supply an essential ecosystem service (ES). Most drylands are expected to experience increasing levels of climatic aridity and land-use pressure in the future. As few studies account for combined effects of these global change drivers, we still have a limited understanding of how these drivers jointly shape forage supply. Here, the concept of social-ecological systems (SESs) is useful, as it helps to formalize the complex interrelationships of drivers. Taking advantage of steep gradients of climatic aridity and land-use pressure in West Africa, a crossed space-for-time substitution was applied to capture combined effects of climate and land-use change on forage supply. We have operationalized the SES concept via structural equation modelling, and analysed how drivers directly or indirectly affected forage quantity, quality and their integrated proxy (metabolisable energy yield). Results demonstrate that contemporary dryland SESs are mainly controlled by land-use, which has often been used as a proxy for other variables, such as climatic aridity. Aridity was also directly linked to a higher risk of vegetation degradation, indicating that future drylands will be less resilient to grazing pressures. The importance of land-use drivers for ES provision implies that sustainable grazing management could potentially mitigate detrimental climate change effects. However, model effects mediated by intermediate variables, such as aridity, short-term vegetation dynamics, and weather fluctuations, make it extremely difficult to predict climate change effects on ESs. Integrating structural equation modelling into the well-defined SES concept is thus highly useful to disentangle complex interdependencies of global change drivers in dryland rangelands, and to analyze drivers' direct and indirect effects on ESs. Our novel approach can thus foster a deeper understanding of patterns and mechanisms driving ecosystem service supply in drylands, which is essential for establishing sustainable management under conditions of global change.

1. Introduction

Livestock rearing is the dominant land-use sector on earth and plays a critical role in human nutrition and food security (Godber and Wall, 2014; Herrero and Thornton, 2013). Approximately 40% of global agricultural gross domestic product is derived from livestock rearing, providing income for more than 1.3 billion people and nourishment for at least 800 million of the world's poor in the developing world (Herrero and Thornton, 2013). Livestock rearing is also the primary type of land-use in drylands, which comprise arid, semi-arid and dry-subhumid ecosystems (Adeel et al., 2005). As drylands support many socially disadvantaged groups that rely heavily on grazing and farming (Godber and Wall, 2014), livelihood security in drylands is highly dependent on the 'forage' ecosystem service that is provided by rangeland vegetation (Adeel et al., 2005; Phelps and Kaplan, 2017). Including livestock production into agricultural activities often compensates for negative effects of climatic, market and disease shocks on livelihood security by diversifying risk and increasing income (Martin et al., 2016;

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https://doi.org/10.1016/j.gloenvcha.2018.08.007
Received 28 March 2018; Received in revised form 30 August 2018; Accepted 31 August 2018
Available online 13 September 2018
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Thornton et al., 2007).

In many dryland regions such as those in Sub-Saharan Africa, increasing local demands for livestock products will also increase demands for forage (Herrero and Thornton, 2013). The expected grazing land expansion and intensification of livestock rearing practices may exert detrimental feedbacks on ecosystem functions and on the supply of ecosystem services (ESs), including forage supply, which implies the quantity as well as quality of forage resources (Guuroh et al., 2018; Reynolds et al., 2007; Vandandorj et al., 2017). Various abiotic and biotic factors may interactively contribute to this 'feedback spiral' towards degradation (King and Hobbs, 2006).

Besides changing land-use, climate change constitutes another severe threat to dryland rangelands worldwide (Maestre et al., 2012; Ruppert et al., 2015). Climate change effects on drylands will be particularly strong, with most drylands projected to experience an increase in precipitation variability, including more extreme rainfall events and intense droughts, and temperature (Maestre et al., 2012). Although it is widely acknowledged that global drivers of change interact, we still have a limited understanding how they shape ES supply through their various interdependencies (Oliver and Morecroft, 2014). In this regard, Guuroh et al. (2018) recently contributed to a better understanding of the relative importance of global change drivers on ES supply, including forage provision, in Sub-Saharan Africa. However, this study was not designed to investigate direct and indirect effects of land-use and climate change on ESs and this remains a critical knowledge gap.

To formalize and disentangle the joint effects of global change drivers on ES provision from dryland rangelands, the concept of social-ecological systems (SESs) is particularly useful (Huber-Sannwald et al., 2012; Linstädter et al., 2016). Within an SES, a dynamic co-adaptation exists between human decision-making and ES provision. Hence, human and ecological subsystems are coupled and interlinked by diverse drivers operating across multiple spatial and temporal scales (Stafford Smith et al., 2007).

Another characteristic of dryland rangelands is the high inter- and intra-seasonal variability in forage supply. Firstly, forage provision in seasonal climates is always subject to periodic fluctuations due to the phenological development of plants (Butt et al., 2011). Secondly, variable weather conditions can trigger substantial short-term vegetation responses, especially at the beginning of the growing season (Brüser et al., 2014). Finally, disturbances such as grazing and fire may cause an immediate loss of plant biomass (Augustine and McNaughton, 2006; Oesterheld et al., 1999). Due to a variety of anthropogenic disturbances overlaying other sources of spatio-temporal variability, spatio-temporal patterns in forage provision are particularly complex in sub-Saharan Africa (Brottem et al., 2014).

Besides the inherent complexity of dryland SESs and the importance of intra-seasonal and short-term variation, there is a third reason for our limited understanding of how global environmental changes modulate ES provision on a regional scale: global change implies changes in multiple biotic and abiotic factors. This hampers the disentanglement of their direct and indirect effects on ecosystem services. In this context, structural equation modelling (SEM) is increasingly applied, as it allows direct and indirect drivers (i.e. the effect that a variable A exerts over a variable B by a mediator variable C), as well as combined effects on target variables to be separated (Eldridge and Delgado-Baquerizo, 2017; Gaitan et al., 2014; Ochoa-Hueso et al., 2018). These effects are usually shown via path diagrams with linkages or pathways between variables.

Identifying such effect pathways and the variables that mediate these effects (via indirect linkages) would support monitoring and early-warning systems to foster adaptive livestock management strategies (Stuth et al., 2005). Furthermore, knowing direct and indirect effects of climate and land-use change on forage supply at a regional level would enhance our ability to understand and predict impacts of global change on this critical ecosystem service (Martin et al., 2014).

To achieve such an understanding, one of the most efficient study approaches is to exploit natural gradients in climate and land-use (Oliver and Morecroft, 2014). Here we take advantage of the fact that in West Africa's Sudanian savannas, a steep regional gradient of climatic aridity is overlain by sharp local gradients of land-use pressure (Ferner et al., 2015; Guuroh et al., 2018; Ouédraogo et al., 2015). Hence, a crossed space-for-time substitution can be used for both climate and land-use change, while previous ES studies typically focussed either on climate change (Valencia et al., 2016; Yuan et al., 2017) or land-use change (Allan et al., 2015) and assessed only a limited set of drivers (Oliver and Morecroft, 2014).

The aim of our study is to assess the simultaneous effects of climate change and land-use change on the quality and quantity of the African drylands' forage supply. Uniquely, our study *formalizes* the direct and indirect effects of global drivers of change through a SES approach, and *quantifies* direct and indirect effects via structural equation modelling (SEM). Three hypotheses were tested: (H1) Combining the SES framework with SEM helps to disentangle causal relationships underlying land-use and climate change effects on forage supply; (H2) SEM also helps to detect feedback pathways of long-term and short-term drivers; and (H3) global environmental change has strong indirect effects on forage supply that can either strengthen or counteract its direct effects.

2. Materials and methods

2.1. Study area

The study area spans northern Ghana to central Burkina Faso, and covers ca. 106 000 km^2 in West Africa's Sudanian savannas (Fig. 1). The climate is characterized by a rainy season from May to August in the north, and April to October in the southeast. The area includes a steep gradient of climatic aridity, ranging from a mean annual precipitation (MAP) of 600 mm in the north to 1200 mm in the southeast (Fig. 1). This corresponds to aridity indices (UNEP, 1997) of 0.31 (semi-arid) to 0.69 (humid) and a precipitation seasonality (coefficient of variation) ranging from 79 to 124 (Hijmans et al., 2005). The main geological units are migmatite in the north and sandstone in the south (Ferner et al., 2015), corresponding to plinthosols and lixisols as the main soil types (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). The Sudanian savannas in the study area are used as low-input rangeland sites (Fig. 1) and constitute a belt of farmed parkland savanna (Maranz, 2009) with > 3000 years of livestock farming (Ballouche and Neumann, 1995). Apart from adjusting the timing and intensity of grazing to forage provision, no rangeland management techniques (such as sowing of legumes or fertilization) are applied. Outside protected areas, recent land-use consists of a mosaic of fallows, non-arable land, forest fragments and fields (Friedl et al., 2010).

2.2. Study design

2.2.1. Social-ecological systems

We used a social-ecological system (SES) perspective (Huber-Sannwald et al., 2012; Linstädter et al., 2016) to asses the dynamic coadaptation between human decision-making and the environment's

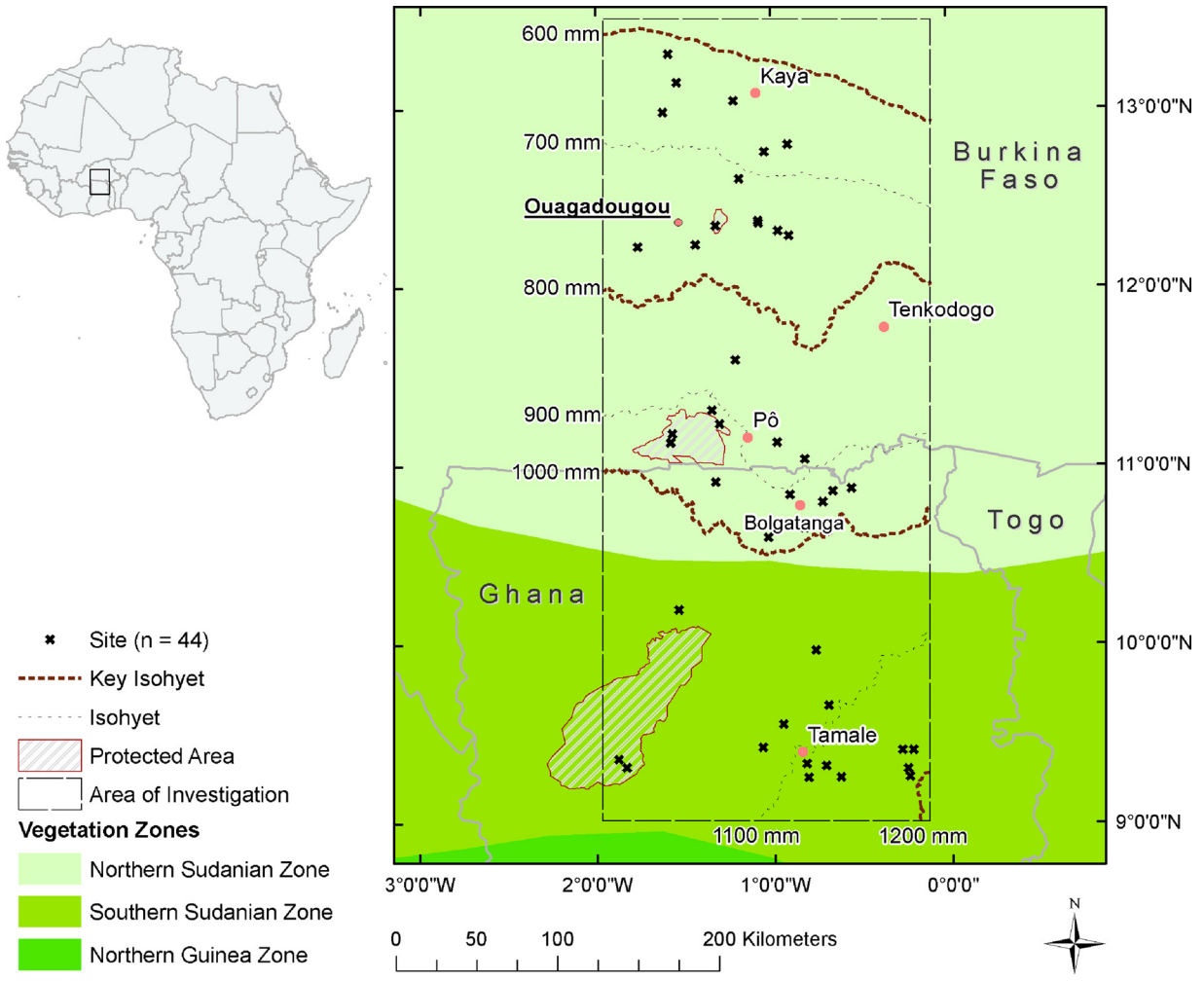

Fig. 1. Map of study area and sites with vegetation zones based on White (1983). The study area was separated into three zones of increasing aridity based on isohyets: 1200–1000 mm = zone 1, 1000–800 mm = zone 2, 800–600 mm = zone 3 (www.worldclim.org). In each zone, the full length of the respective land-use pressure gradient was sampled, ranging from ungrazed sites in protected areas over moderately grazed sites to heavily grazed sites close to settlements.

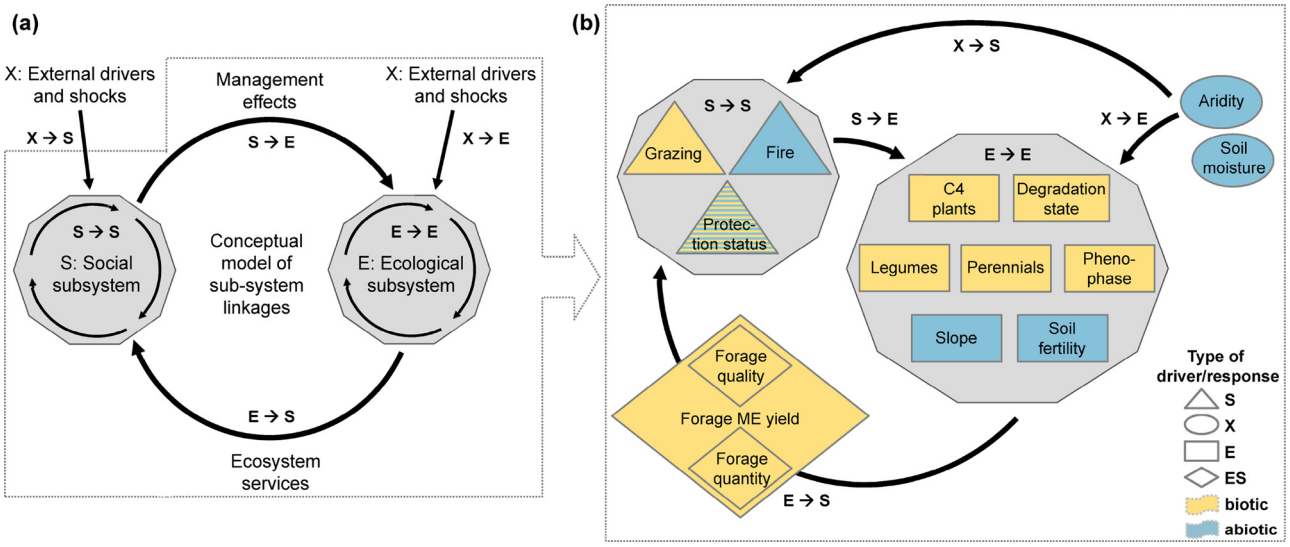

Fig. 2. Conceptual framework for studying interactive effects of climate change and land-use change on ecosystem services. (a) Six types of interdependencies are distinguishable within a complex social-ecological system (SES); modified from Stafford Smith et al. (2007): Interactions within the social subsystem (S→S) and the ecological subsystem (E→E) are accompanied by linkages between subsystems, i.e. land-use effects (S→E) and ecosystem services (E→S). Furthermore, external drivers and shocks may affect the social (X→S) and the ecological subsystem (X→E). (b) This study explores how these interdependencies modulate the ecosystem service of forage provision (E→S) in dryland rangelands under conditions of global change. It considers climate change effects on both subsystems (X→E, X→S) and land-use change effects on the ecological subsystem (S→E). The driver 'protection status' combines biotic as well as abiotic effects.

provision of ecosystem services. Hence, we distinguished between a SES's human and ecological subsystem; these are coupled and interlinked by diverse drivers operating across multiple scales (Stafford Smith et al., 2007). According to the SES framework proposed by Stafford Smith et al. (2007), three types of drivers are distinguishable, resulting in six possible interdependencies (Fig. 2a). These are ecological drivers (E) which interact within the ecological subsystem (E→E); external drivers and shocks (X) that directly affect the ecological (X→E) or social subsystem (X→S); and land-use drivers (S) which interact within the social subsystem (S→S) or constitute a linkage between the social and the ecological subsystem (S→E). Together these drivers determine vital ESs including forage provision (Bennett et al., 2009; Duru et al., 2015) and thus a key ecological-to-social linkage (E→S). Besides filling the 'black box' of interactions within the ecological subsystem (E→E), our study mainly addresses the question of how global change drivers – with climate change as an external driver (X) and land-use change as a social driver (S) – shape ecosystem characteristics and ES supply through their various interactions (Fig. 2b).

2.2.2. Sampling design

Our sampling design intended to capture land-use and topo-edaphic gradients along the regional climatic gradient. For this purpose, our sampling was stratified into three zones of climatic aridity based on isohyets (Fig. 1). In each climate zone, the full length of the respective land-use gradient was covered by including heavily grazed sites near settlements as well as non-grazed sites in protected areas. Sites were also distributed over the main geological units in each zone to capture soil diversity. Sampling at the sites was further stratified by topographic position (upslope, footslope and lowland) to capture local terrain differences and their effects on plant-available water due to water runoff and runon (Nacoulma et al., 2011). Field data were collected during the rainy seasons 2012 (June–September) and 2013 (July–October) to include both inter- and intra-seasonal dynamics of forage provision. To capture the spatio-temporal variability of various biotic and abiotic drivers, we combined data publicly available at the site level with data recorded at the level of vegetation plots (Table 1, see also Table C1 in Appendix C). Here, most variables affecting the savanna ecosystem (e.g., fire) were acquired from GIS data, while data describing interactions within the ecosystem (e.g., phenophase) were predominantly collected in the field at the (sub-) plot level. We sampled 44 sites along the study area; 14 in the most arid zone, 15 in the intermediate zone and 15 in the least arid zone. Each site accounted for 3–5 plots (10 m × 10 m) located at different slope positions within rangelands (i.e. fallows that had not been cultivated for > 10 years, or non-arable land; Ouédraogo et al. (2015)), obtaining a total of 302 plots. Finally, three circular subplots of 1 m^2 were randomly placed in each plot. See details on the variables measured at the site, plot and subplot level below.

2.3. Data acquisition

2.3.1. External drivers (X)

Data on climate and weather fluctuations were obtained at the site level, assembling several datasets. From the WorldClim database (www.

Table 1
Characteristics of variables belonging to four variable sets considered in this study (land-use drivers, external drivers (climate and weather drivers), internal drivers within the ecological subsystem, and ecosystem services), and variable affiliation to a 'latent variable' (LV) in structural equation models. Data source is coded as OD = own data and PA = publicly available data. Spatial scale refers to the spatial level of available data, while temporal scale refers to the time span between a change of a driver and the responses of the ecosystem service 'forage'. Minimum, median and maximum values are given if applicable. For further information, see Table C1 (Appendix C).

Variable	LV affiliation	Data source	Spatial scale	Temporal scale of response	Type of variable/unit[a]	Min	Median	Max
Land-use drivers (S)								
Grazing pressure	Grazing	OD	Plot	Months to years	Ordinal (0–4)	0	2[a]	4
Fire frequency	Fire	PA	Site	Years	Events 10 km^{-2} $Year^{-1}$	0	1.11	57.45
Protection status	Protection	PA	Site	Years	Factor (yes/no)	–	–	–
External drivers (X)								
Aridity index	Aridity	PA	Site	Decades	Relative	0.31	0.48	0.69
Climate zone	Aridity	PA	Site	Decades	Ordinal (1–3)	1	2[a]	3
Mean annual precipitation	Aridity	PA	Site	Decades	mm	631	932	1200
Potential evapotranspiration	Aridity	PA	Site	Decades	mm day^{-1}	1822	1918	2024
Precipitation of driest quarter	Aridity	PA	Site	Decades	mm	0	7	19
Temperature seasonality	Aridity	PA	Site	Decades	SD 100	152.2	184.5	234.0
Accumulated soil moisture	Soil moisture	PA	Site	Days to weeks	%	0	42	83
Soil moisture	Soil moisture	PA	Site	Days to weeks	%	0	14	28
Internal drivers (ecosystem characteristics; E)								
Relative abundance of C_4 plants	C4 plants	OD	Plot	Years	%	0	0.61	0.99
Degradation	Degradation state	PA	Site	Years to decades	RS	0	0	0.0078
Relative abundance of legumes	Legumes	OD	Plot	Years	%	0	0.061	0.83
Relative abundance of perennials	Perennials	OD	Plot	Years	%	0.002	0.45	1
Community-aggregated phenology	Phenophase	OD	Plot	Weeks	Ordinal (0-5)	1.06	2.37[a]	4.93
Slope position	Slope	OD	Plot	Millennia	Ordinal (0-3)	1	2[a]	3
Soil C content	Soil fertility	OD	Plot	Weeks	%	0.29	1.08	4.71
Soil N content	Soil fertility	OD	Plot	Weeks	%	0.031	0.071	0.32
Ecosystem services								
Metabolisable energy	Forage quality	OD	Plot	–	MJ kg^{-1} DM	3.47	9.03	14.71
Total aboveground biomass	Forage quantity	OD	Plot	–	g m^{-2}	22.08	121.8	655.2
Metabolisable energy yield	Forage ME yield	OD	Plot	–	GJ ME ha^{-1}	2.27	11.03	55.22

SD = Standard deviation; CV = Coefficient of variation; RS = Residuals.
[a] Ordinal data were treated as quasi-numerical.

worldclim.org), climate variables such as mean temperature, MAP, and precipitation seasonality were derived (Table 1). We further calculated aridity indices (UNEP, 1997) using the formula by Thornthwaite (1948) and extracted data on potential evapotranspiration from CGIAR-CSI Global-Aridity and Global-PET Database (Trabucco and Zomer, 2009) using the formula by Hargreaves et al. (1985).

In contrast to the general long-term phenomenon of an arid climate, intra-seasonal weather fluctuations were captured as short-term changes in soil moisture. This was estimated via two variables acquired from NASA (Owe et al., 2008) based on passive microwave remote sensing. We acquired soil moisture for the fieldwork data collection day (interpolated if necessary), as well as 'accumulated soil moisture' for the fieldwork data collection day and two preceding days.

2.3.2. Ecosystem properties (E)

Vascular plant species were recorded with their phenological stage, cover and average height at the subplot level by visual interpretation, and were subsequently averaged to plot level. Six phenological stages (germinating, sprouting, shooting, flowering, fruiting, and senescent) were distinguished, using a simplified BBCH scale (Hess et al., 1997). Species' biovolume data (cover × height) and phenological stage were aggregated into communities' phenological stage ('phenophase'), following procedures for community-aggregated traits (Vile et al., 2006). We also grouped species' biovolume data into the biovolume of (i) legumes versus non-legumes, (ii) annuals versus perennials, and (iii) species with a C_4 photosynthetic pathway versus non-C_4 species.

At the plot level, topsoil samples (0–4 cm) were assembled from five randomly placed subsamples to determine carbon (C) and nitrogen (N) content. Moreover, negative RESTREND (Global Residual Trend of Sum Normalized Difference Vegetation Index; Wessels et al. (2007)) values were used as a proxy for human-induced degradation at the site level. Degradation severity was calculated as the negative residuals of a regression between annual rainfall and annual sum NDVI. If the sum NDVI was lower than expected in response to received rainfall, a reduced rain-use-efficiency and thus vegetation degradation could be assumed. Here, NDVI values will integrate the effects of a variety of different drivers on vegetation growth and health.

2.3.3. Land-use (S)

At the plot level, visible signs of herbivore activities (trampling, droppings, and the removal of standing biomass) were used for an expert estimate of recent grazing pressure (following Linstädter et al., 2014); ranging from 0 (ungrazed) to 4 (heavily grazed). Sites were defined as being protected according to the classification by IUCN and UNEP-WCMC (2013). Fire frequency data were acquired from MODIS Active Fire Detections extracted from MCD14ML distributed by NASA FIRMS.

2.3.4. Forage provision (ES)

As forage quality (i.e. metabolisable energy content; ME; Table 1) is time and cost intensive to sample, we estimated the ME content of plots by applying partial least squares regression (PLSR; Wold et al. (2001)) parameterized with vegetation reflectance obtained from a full-range spectrometer (FieldSpec 3 Hi-Res Portable Spectroradiometer; ASD Inc., Boulder, CO, USA). The regression was established for the same research area and found to be robust (R^2 of 0.56 and errors of 11.7% in validation), allowing their use here as a dependent variable (see Ferner et al. (2015) for further information).

Total aboveground biomass (tBM) was used as a proxy for forage quantity (Oomen et al., 2016). Based on species' biovolume, phenology and functional group affiliation, linear models were used to estimate tBM per subplot (for details on methodology see Guuroh et al. (2018)). We also calculated the product of forage quality and quantity as an integrative proxy of forage supply from rangelands (metabolisable energy yield, MEY). All tBM, ME and MEY calculations were carried out per subplot and then averaged to plot level.

2.4. Data analysis

To disentangle joint effects of global change and land-use drivers on forage provision, Partial Least Squares Path Modelling (PLS-PM; Tenenhaus et al. (2005)) was used, a non-parametric, composite-based type of structural equation modelling (SEM). SEMs are multivariate methods that allow the linkage of measurable attributes (i.e. indicator variables) to underlying hypotheses or theoretical concepts by means of (unobserved) latent variables (LV). LVs are constructs of predictors or indicators merged, in this particular case based on correlations, into a single robust variable or component (i.e. similar to the components of PCA or CCA, but in a supervised manner).

Path models can also quantify direct, indirect and combined effects on target variables (Grace et al., 2010). In PLS-PM, this is done by performing linear regressions for each interaction, obtaining model coefficients (i.e. path coefficients (β)). Indirect effects are exerted by modulating intermediate variables, and can either strengthen a driver's direct effect (unidirectional effects; i.e. with same signs of path coefficients), or weaken them (opposing effects, i.e. different signs of path coefficients). Even when SEM presented similar model accuracies to regressions and ordinations methods, the modulation of the intermediate effects demonstrated a higher potential for the identification of key functioning parameters (Grace, 2003). Up to now, PLS-PM has been used mainly in the social sciences, but also has demonstrated applicability in the geosciences (Lopatin et al., 2015). See Table 1 for the composition of the LVs and their indicators.

Through SEM, the complex network of all important interactions between driver and response variables were modelled. This included the calibration of three separate sub-models to capture relationships between the three main driver types. To understand the direct and indirect effects of drivers on ecosystem service provision, we finally calibrated separate sub-models for our three proxies of forage provision. Here, a positive path coefficient indicates a positive relation between drivers or between drivers and the ES of forage supply while a negative path coefficient indicates a negative relationship.

Since SEM results depend on the specification of underlying hypotheses (Grace et al., 2010), expert knowledge was required to build a conceptual *a priori* model and all environmental predictor variables included in the model where selected based on a rigorous literature review of the main processes affecting forage supply. Our final path model (Table C2 in Appendix C) specifies all hypothesized linkages between LVs and forage provision based on the findings of previous studies in (African) rangelands.

Concerning management effects on the ecological subsystem (S→E), it has been found that grazing (Moreno García et al., 2014), fire (Colombaroli et al., 2014; Koerner and Collins, 2014), and protection (Traoré et al., 2012) can significantly shape vegetation structure, composition and the nutritional quality of forage. Fire was defined as a driver of the social subsystem rather than the ecological subsystem because most fires in West Africa are anthropogenic (Gregoire and Simonetti, 2010), e.g. they are used as a management tool within the protected areas of Nazinga Classified Forest (Mäkelä and Hermunen,

2007) and Mole National Park (Sackey and Hale, 2008). These protected areas (one within each climate zone) represent reference sites for a near-natural state of savanna vegetation as they feature different vegetation species, e.g. perennial grasses and a dense tree layer. Moreover, external drivers (X→E) such as climatic aridity can also influence vegetation composition and structure (Barthelemy et al., 2015; Gaitan et al., 2014). Here we chose to focus on temperature and precipitation since they are known to primarily influence plant growth. Within the ecological subsystem (E→E), it can be anticipated that plants vary in forage quality and quantity depending on their photosynthetic pathway (Sage and Kubien, 2003), N-fixing ability (Phelan et al., 2015) and life cycle (Le Houérou, 1980; Ruppert et al., 2015).

Due to data availability and model structure, all LVs were defined as endogenous, i.e. dependent on at least one exogenous (independent) LV, except protection, aridity, soil moisture and slope, which were defined as independent exogenous variables. As data was acquired at different spatial scales, and since drivers operated on varying temporal scales (Table 1), an additional rule set was formulated. First, no LV measured at plot level was expected to have an influence on LVs from site level, except for grazing pressure, which was considered to represent an attribute true for a larger area. Second, soil moisture, as an external LV that is highly variable in space and time, was expected to only influence the response variables, which we assumed would respond within days to weeks (Table 1). Lastly, LVs that usually remain stable over several years (protection, fire frequency, aridity, degradation, and slope) were not expected to alter plant phenology during the study years.

For PLS-PM model validation, bootstrapping was performed with 1500 repetitions. All statistical analyses were undertaken in R (R Development Core Team, 2011). Path model fitting and analysis was primarily carried out through the 'plspm' package (Sanchez, 2013).

3. Results

3.1. Causal relationships shaping the social-ecological systems

Complex relationships shaping the studied SESs were found (Fig. 3). Considering land-use drivers (Fig. 3a), the strongest effects were found between drivers themselves (S→S), i.e. between protection and grazing pressure (−0.55) and protection and fire frequency (0.37). The various land-use effects on ecosystem characteristics (S→E) were all negative in nature, with particularly strong effects of grazing on phenophase (−0.20), but with almost no fire effects.

The external climatic driver 'aridity' had by far the most important and most diverse effects in studied SESs (Fig. 3b), while 'soil moisture' demonstrated only non-significant effects. Aridity did not only influence the ecological subsystem directly but also indirectly via several feedback pathways. Specifically, it modulated two management interventions (X→S): Increasing aridity increased grazing pressure (0.27) but decreased fire frequency (-0.16). Hence, strong and direct interactions between climate and land-use drivers were found. Direct aridity effects on ecosystems (X→E) included a negative effect (−0.35) on the abundance of perennial plants and a positive effect (0.27) on C_4 plants. Aridity also increased the likelihood of vegetation degradation (0.33).

Several interdependencies were discernible within the ecological subsystem (Fig. 3c; E→E). Abiotic factors only affected biotic factors (e.g., soil fertility increased perennial plant abundance). In contrast, biotic factors could either interact between themselves – with high C_4 plant abundance decreasing legume abundance (−0.27) – or by feedback on abiotic factors. Importantly, vegetation degradation had negative effects on soil fertility.

3.2. Important drivers of the ecosystem service of 'forage supply'

Separate models for forage quality, quantity and their combination (MEY) explained 45%, 70% and 52% of variation, respectively (Fig. 4). With respect to global change drivers, we found that climatic aridity had no direct impact on any aspect of forage supply. However, it did have a negative impact on forage quality, although slightly under the threshold for significance. Among land-use drivers, grazing pressure had strong, contrary effects on forage quality and quantity (ME: 0.23, tBM: −0.27). Unsurprisingly, protection had opposite effects, but was only significant for tBM (0.4) and MEY (0.33). Fire frequency had no significant effects on forage provision.

Besides global change drivers, seasonal vegetation dynamics (phenophase), weather fluctuations (soil moisture) and degradation state were also significant drivers of forage supply, while other ecosystem characteristics such as slope position and abundance of perennials were of minor importance. Like grazing, phenophase also had contrary effects on forage quantity and quality (ME: −0.24, tBM: 0.31).

3.3. Direct and indirect controls of forage supply

Indirect effects of global change drivers on forage supply were often strong; in the case of protection and climatic aridity, they were even stronger than their direct effects. With respect to effect direction, considerably more unidirectional effects (indirect effects strengthening direct effects) were observable than opposing effects (indirect effects weakening direct effects; see Fig. 5). Protection was the most important indirect driver, reducing forage quality via its effects on two other land-use drivers, but increasing forage quantity and MEY. Interestingly, the most notable opposing effect occurred regarding climatic aridity. Stronger indirect effects always reversed its small, non-significant, direct effects on forage supply (negative on ME, positive on tBM and MEY).

4. Discussion

4.1. Disentangling causal relationships in the study SESs

We found complex relationships within the studied SESs. First, strong interdependencies within the social subsystem were found (S→S). The negative effect of protection on grazing pressure seems trivial, as livestock grazing is prohibited within protected areas. However, we observed that this law is increasingly violated (also confirmed by previous studies; Ouédraogo et al. (2015); Traoré et al. (2012)). Positive protection effects on fire incidence can be explained by a higher fire frequency within protected parks (Gregoire and Simonetti, 2010) due to regular management fires (Ouédraogo et al., 2015).

Second, multiple effects of land-use drivers on ecosystem characteristics were detected (S→E). The strong negative effect of grazing on phenophase can be explained by rejuvenation after disturbance (Breedt et al., 2013). In contrast, fire effects on ecosystem characteristics were non-significant, probably due to the fact that fire tends to have positive effects on ecosystem functions in more humid areas and negative effects under more arid conditions (Oesterheld et al., 1999).

Third, climatic aridity primarily shaped the ecological subsystem as an external filter (X→E). It had negative effects on perennial plants and C_3 plants, which is in line with previous observations that aridity

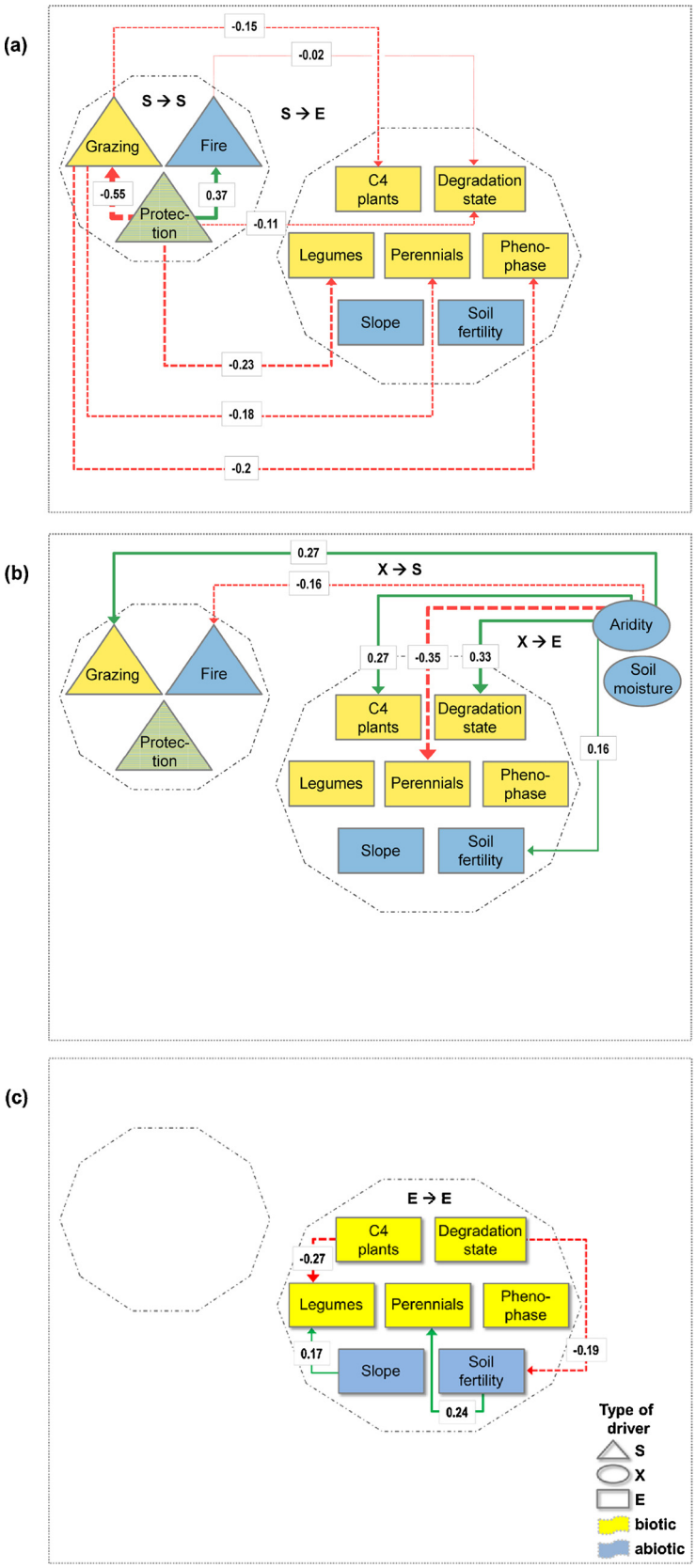

Fig. 3. Sub-models for relationships within studied SESs, with (a) drivers within the social subsystem (S→S) and social-to-ecological drivers (S→E), (b) external-to-social (X→S) and external-to-ecological drivers (X→E), and (c) ecological-to-ecological drivers (E→E; see Fig. 3). Pathways between drivers are shown in green-solid to indicate positive relations, and in red-dashed for negative relations. Arrow widths are proportional to path coefficients (showing drivers' standardized direct effects) given on the arrow. Only significant effects are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

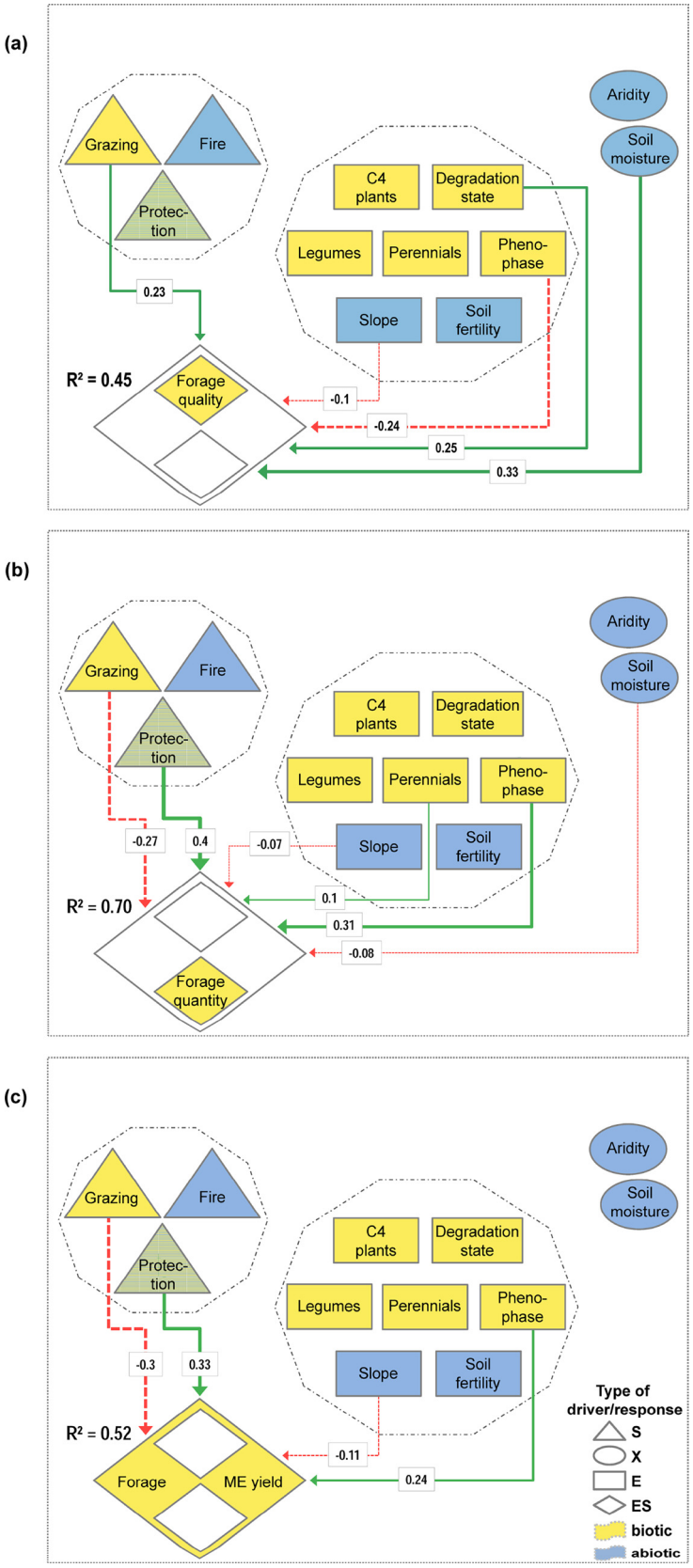

Fig. 4. Final SEMs for (a) forage quality (ME), (b) forage quantity (tBM) and (c) forage ME yield (MEY). Path coefficients on the arrows, as well as arrow size, show the strength of effects. Green-solid arrows indicate positive causal relations, while red-dashed arrows depict negative relations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

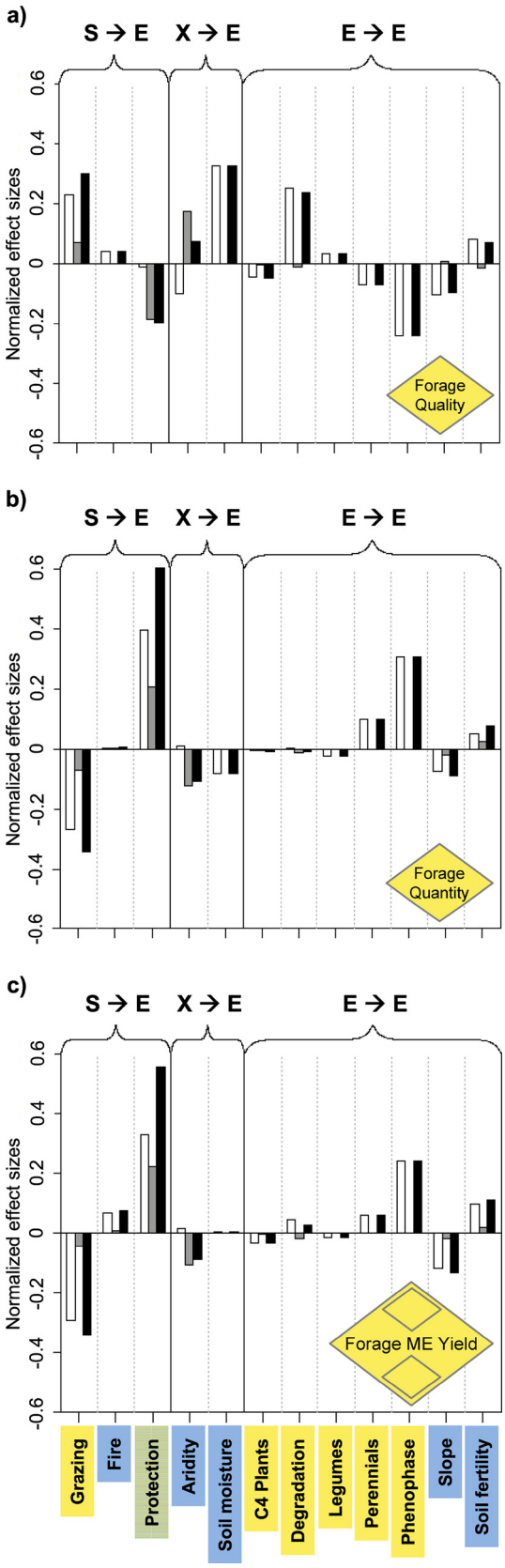

Fig. 5. Normalized direct (white), indirect (grey) and total effects (black) of driver variables in SEMs on (a) forage quality, (b) forage quantity and (c) forage ME yield.

favours annuals (Linstädter et al., 2014) and heat-adapted C_4 plants (Sage and Kubien, 2003). Climatic aridity was also directly linked to the incidence of vegetation degradation, underlining the vulnerability of more arid regions to degradation (Adeel et al., 2005). Note that the RESTREND method statistically removes effects of precipitation changes on rain-use-efficiency, allowing a focus on human-induced degradation (see Fensholt et al., 2013; Wessels et al., 2007). Moreover, climatic aridity was found to be an important mediator of land-use drivers (X→S), most notably grazing pressure. This underlines that these key drivers of global change are not independent (Munson et al., 2016; Oliver and Morecroft, 2014; Turner, 1998). For example, livestock keeping is more common under arid conditions, where grazing allows the utilization of land not suitable for cropping (Fetzel et al., 2017).

Finally, in the ecological subsystem (E→E), the negative effect of C_4 plants on legumes was particularly strong. This is not surprising, as perennial C_4 grasses dominate the grass layer of protected areas (Bocksberger et al., 2016; Zimmermann et al., 2015). In contrast, legumes may only gain dominance under conditions of overgrazing, when they are no longer outcompeted by perennial grasses (Linstädter et al., 2014).

4.2. Effects of drivers with short-term and long-term variation

We used a crossed space-for-time substitution to capture interactive effects of climate and land-use change on forage attributes. As these drivers can affect forage provision at different spatial and temporal scales (Linstädter et al., 2016), it was intended to capture both short- and long-term variation. We could thus compare the effects of global change drivers acting over comparatively large temporal scales to short-term effects of weather fluctuations and vegetation dynamics. Among drivers of the first type, grazing and protection were particularly important. Grazing increased forage quality by stimulating the regrowth of high-quality plant biomass (Changwony et al., 2015; Moreno García et al., 2014). Additionally, grazing can trigger a shift towards plant communities dominated by palatable and nutritious forage plants, creating 'grazing lawns' (Hempson et al., 2015). Lawn grasses feature high leaf-to-stem ratios, foliar N levels (Moreno García et al., 2014) and thus a high digestibility (Chaves et al., 2006).

Grazing and protection were also important drivers of forage quantity and MEY. While Flombaum et al. (2017) corroborate this result, Guuroh et al. (2018) found the season's accumulated precipitation to be the most important driver of tBM. It was found that grazing negatively affects forage quantity, which is in line with a meta-analysis of dryland rangelands' biomass production (Ruppert et al., 2012). As we did not control for grazing offtake, this partly reflects the direct loss of biomass through grazing (Oesterheld et al., 1999). Moreover, factors such as intra-seasonal biomass turnover and compensatory growth were not accounted for (Fetzel et al., 2017). Therefore, standing biomass is only a rough proxy of biomass production (Oomen et al., 2016).

The strong influence of degradation on forage quality could be explained by the method we used for degradation assessment: based on a regression between annual rainfall and NDVI (Wessels et al., 2007). A low NDVI response to received rainfall implies a reduced rain-use-efficiency and thus human-induced degradation, most likely caused by high grazing pressure (Rasmussen et al., 2014) which increases forage quality.

Among drivers with short-term variation, plant phenology and soil moisture were particularly important for forage supply. Phenology strongly reduced forage quality (e.g. Guuroh et al., 2018), being the

most important factor modulating forage quality of tropical pastures due to a progressive decline in digestibility and crude protein (Atta-Krah and Reynolds, 1989; Changwony et al., 2015). Hence, management strategies like grazing or mowing that counteract phenological progress often improve forage quality (Hughes et al., 2013). Phenology was found to have strong effects on forage quantity, reflecting biomass accumulation in the growth period.

We observed only a small, negative relationship between soil moisture and biomass, contrary to the known influence of stochastic seasonal fluctuations in rainfall and soil moisture on primary production in dryland grasslands (Lauenroth and Sala, 1992). We assume that reduced soil moisture at the end of the rainy season (i.e. at the time of maximum biomass accumulation) is responsible for this effect.

4.3. Strength and direction of global change drivers' indirect effects

As expected from previous studies applying structural equation modelling to quantify global change drivers on ES supply (Allan et al., 2015; Gaitan et al., 2014), we found important indirect effects in the model. Notably, a higher aridity indirectly reduced biomass production and metabolisable energy yield via altered land-use practices. Thus, understanding climate change effects on forage supply requires consideration of complex feedback pathways in dryland SESs (Linstädter et al., 2016), especially (but not solely) via aridification effects on land-use. Although we could not include all climatic aspects of aridity (e.g. radiation), we are certain that all variables considered in the model, which were also selected based on public accessibility, capture the main sources of environmental variation in our study area. Radiation was not included because firstly, it was not expected to vary much *within* sites as the geomorphology within our research area was always gently undulating; secondly, variation of radiation *between* sites should be already captured by including co-varying variables like potential evaporation (Donohue et al., 2010) in the latent variable 'Aridity'; and thirdly, due to an inverse temporal relationship between radiation and rainfall in the research area (Berger et al., 2019), we indirectly accounted for temporal variations of radiation by considering short-term changes in soil moisture.

5. Conclusion

Altogether, our results suggest that our novel SES framework, operationalized via structural equation modelling, greatly helps in disentangling complex effects of global change on ecosystem service supply. The approach helps to find effects of key mediator variables on the whole system which would otherwise not be easily measured. With respect to climate change mitigation, the use of sustainable grazing management practices could potentially mitigate the detrimental effects of increased climatic aridity (see Guuroh et al. (2018)). Here, resting of rangeland vegetation during critical time windows is most promising. This includes resting in post-drought years to prevent (further) rangeland degradation (Müller et al., 2015), and resting in high-rainfall years to facilitate regeneration (Linstädter et al., 2013; Müller et al., 2007). Within a year, resting during early stages of the growth period is also an important tool to avoid degradation (Briske et al., 2011). Resting can be achieved via an adaptive regulation of stocking densities on a local and regional scale; rotational grazing is particularly suitable on a local scale (Briske et al., 2011). To allow resting in drought and post-drought years, grazing reserves or adjusted supplementary feeding strategies are good options (Reed et al., 2015; Schulze et al., 2016). Nevertheless, the presence of indirect feedback pathways, short-term weather fluctuations, and vegetation dynamics make it difficult to upscale and predict global change effects on ESs. Hence, early-warning systems need to capture interdependent effects of changing climate and land-use on ES supply at an appropriate spatial and temporal resolution.

Funding

This work was supported by the German Federal Ministry of Education and Research (BMBF) through WASCAL (grant number FKZ 01LG1202A) and the German Research Foundation (DFG) through the TRR 228 (grant number 398498378). The sponsors had no involvement in study design, in the collection, analysis and interpretation of data, in the writing of the report, and in the decision to submit the article for publication.

Acknowledgements

We are grateful to all farmers who granted us access to their rangelands. The logistical support of the WASCAL Competence Centre in Ouagadougou (in particular Igor Bado) is greatly appreciated. Our thanks also go to Guido Lüchters for statistical advice, to Kristijan Čanak for helpful discussions, and to Joanna Pardoe for improving the English. The authors acknowledge valuable comments of two anonymous reviewers.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.gloenvcha.2018.08.007.

Appendix C

Table C1
Overview of predictor (latent) variables for structural equation modelling (SEM), sorted by driver/response types (Table 1). The associated indicators (and sources) used to model forage provision (ME, tBM, MEY) are also listed. Please note that information is derived at different scales; if not indicated otherwise, data is acquired at site (village) level. Data analysis was done for the years 2012–2013.

Latent variable	Drivers of the social subsystem (S)
	Indicator 1
Grazing	**Grazing pressure** Expert estimation of recent grazing pressure using visible signs of herbivore activities including trampling, droppings, and the removal of standing biomass (following Linstädter et al., 2014); ranging from 0 (ungrazed) to 4 (heavily grazed).
Fire	**Fire frequency** Data on fire events from 1 st November 2008 to 31 st October 2013 were acquired from MODIS Active Fire Detections extracted from MCD14ML distributed by NASA FIRMS (Available online at https://earthdata.nasa.gov/active-fire-data). Fire events were normalized by calculating fire frequencies per km^2 and year at each site from a 5 km buffer around the village centre.
Protection	**Protection status** Protected areas as defined by IUCN and UNEP-WCMC (2013), including Gonse and Nazinga (classified forests) in Burkina Faso and Mole (national park) in Ghana.

Latent variable	External drivers (X)						
	Indicator 1	**Indicator 2**	**Indicator 3**	**Indicator 4**	**Indicator 5**	**Indicator 6**	**Indicator 7**
Aridity	**Climate zone**	**Aridity index**	**Pot. evapotrans-piration [mm day^{-1}]**	**Temperature seasonality**	**Mean annual precipitation [mm]**	**Precipitation seasonality**	**Precipitation of driest quarter [mm]**
	The investigation area was separated into three zones based on isohyets (1000-1200 mm = zone 1, 800-1000 mm = zone 2, 600-800 mm = zone 3).	UNEP aridity indices (UNEP, 1997) were calculated as the ratio of annual average precipitation to potential evapotranspiration (P/PET) based on WorldClim (Hijmans et al., 2005) precipitation data and potential evapotranspiration data (see Indicator 3).	Monthly averages of potential evapotranspi-ration over the period 1950-2000 were extracted from CGIAR-CSI Global-Aridity and Global-PET Geospatial Database (Trabucco and Zomer, 2009).	Standard deviation *100 based on monthly values; from WorldClim (Hijmans et al., 2005) climate data.	Data from World Clim (Hijmans et al., 2005) climate data.	Coefficient of variation based on monthly values; from WorldClim (Hijmans et al., 2005) climate data.	Data from WorldClim (Hijmans et al., 2005) climate data.
	Indicator 1			**Indicator 2**			
Soil moisture	**Soil moisture [%]** Data from day of measurement from NASA LPRM/TMI/TRMM Daily L3 Day Surface Soil Moisture (Owe et al., 2008) derived from passive microwave remote sensing data from the Tropical Rainfall Measuring Mission (TRMM) Microwave Imager (TMI), using the Land Parameter Retrieval Model (LPRM). If necessary, data was interpolated by spatio-temporal interpolation using R package 'spacetime' (Pebesma, 2012).			**Accumulated soil moisture [%]** See Soil moisture; data was summed up over three days (two days before data collection and day of data collection)			

Latent variable	Drivers of the ecological subsystem (E)
	Indicator 1
C4 plants	**Relative biovolume of plant species with C4 photosynthesis pathway [%]** Based on vegetation relevées (Guuroh et al., 2018), the relative biovolume of plant species with C4 photosynthesis pathway (averaged per plot) was calculated.
Degradation state	**RESTREND**

(*continued on next page*)

Table C1 (*continued*)

Latent variable	Drivers of the ecological subsystem (E)	
	Global Residual Trend of Sum NDVI (RESTREND) 1981-2003 published by UN FAO via GeoNetwork. Wessels et al. (2007) proposed a method to avoid the correlations between rain-use efficiency and rainfall to better distinguish land degradation from the effects of rainfall variability. First, a regression between observed sum NDVI (measured by Advanced Very High Resolution Radiometer (AVHRR)) and rainfall was established for each pixel, i.e. a model predicting sum NDVI using rainfall data. The model´s residuals (i.e. differences between observed and predicted sum NDVI) for each pixel were extracted and analysed by linear regression. In our study, only negative trends were considered (i.e. only degradation not recovery).	
Legumes	**Relative biovolume of leguminous species in vegetation clusters [%]** Based on vegetation relevées (Guuroh et al., 2018), the relative biovolume of leguminous plant species (averaged per plot) was calculated.	
Perennials	**Relative biovolume of perennial plant species [%]** Based on vegetation relevées (Guuroh et al., 2018), the relative biovolume of perennial plant species (averaged per plot) was calculated.	
Phenophase	**Phenology** Based on species-specific biovolume and phenological stages, community-weighted phenology was calculated at subplot level and averaged at plot level (Guuroh et al., 2018). Phenology values are 1 = Shooting, 2 = Sprouting, 3 = Flowering, 4 = Fruiting, 5 = Senescent.	
Slope	**Slope position** Slope position along topographic transect, i.e. lowland (1), footslope (2) and upslope (3) (Guuroh et al., 2018).	
	Indicator 1	**Indicator 2**
Soil fertility	**N content [%]** Result of soil analysis at plot level (Guuroh et al., 2018).	**C content [%]** Result of soil analysis at plot level (Guuroh et al., 2018).

Latent variable	Ecosystem services (ES)
	Indicator 1
Forage quality	**Forage quality [MJ kg^{-1} DM]** Metabolisable energy (ME) estimated from spectral reflectance data of vegetation using a statistical model calibrated in the same research area (Ferner et al., 2015).
Forage quantity	**Forage quantity [g m^{-2}]** Total biomass (tBM) estimated from height and cover values of plant species using a statistical model calibrated in the same research area (Guuroh et al., 2018).
Forage ME yield	**Forage ME yield [GJ ME ha^{-1}]** Combination of forage quality and quantity (MEY, Islam et al. (2011)) calculated by multiplying ME and tBM and dividing by a factor of 1000.

Table C2
The conceptual path model in the form of an interaction matrix indicating all pathways between drivers that remain in SEM after applying the defined rule set based on expert knowledge. The matrix is read as 'columns affecting rows'; i.e. a cross in the cell x; y (x-th column and y-th row) means that column x could affect row y. Since no driver can affect itself, the diagonal of the matrix is empty. The cells above the diagonal are also empty since SEM is a recursive model (no loops are allowed within the inner model).

	Aridity	Slope	Protection	Soil moisture	Grazing	Fire	Degradation	Soil fertility	Phenophase	C4 plants	Legumes	Perennials
Aridity												
Slope												
Protection												
Soil moisture												
Grazing	X	X	X									
Fire	X		X		X							
Degradation	X		X		X	X						
Soil fertility	X	X	X		X	X	X					
Phenophase					X							
C4 plants	X	X	X		X	X	X	X				
Legumes	X	X	X		X	X	X	X		X		
Perennials	X	X	X		X	X	X	X		X	X	

Tab. A2 The conceptual path model in the form of an interaction matrix indicating all pathways between drivers that remain in SEM after applying the defined rule set based on expert knowledge. The matrix is read as 'columns affecting rows'; i.e. a cross in the cell x; y (x-th column and y-th row) means that column x could affect row y. Since no driver can affect itself, the diagonal of the matrix is empty. The cells above the diagonal are also empty since SEM is a recursive model (no loops are allowed within the inner model).

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